

# A NEW SPECIES, *ADAMSIA OBVOLVA* (CNIDARIA: ANTHOZOA: ACTINIARIA), FROM THE GULF OF MEXICO, AND A DISCUSSION OF THE TAXONOMY OF CARCINOECIUM-FORMING SEA ANEMONES

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## ABSTRACT

*Adamsia obvolva* is a new species of sea anemone (order Actiniaria, family Horathiidae) from the Gulf of Mexico, symbiotic with the hermit crab *Parapagurus pictus* (Smith, 1883). The pedal disc of the anemone enwraps the gastropod shell in which the hermit crab lives, and secretes a thin, chitinous carcinoecium that lies between the pedal disc ectoderm of the anemone and the gastropod shell. The description of *A. obvolva* n. sp. highlights many of the problems confounding the systematics of actinarians symbiotic with hermit crabs. *Adamsia obvolva*, which has been misidentified as *Paracalliactis involvens* (McMurrich, 1893), presents a suite of attributes that blur the distinction between the genera *Adamsia* Forbes, 1840, and *Calliactis* Verrill, 1869. We review definitions of these genera and emend *Adamsia* to include only those species that form a carcinoecium and have a lobed pedal disc. To better differentiate between *A. obvolva* and *P. involvens*, we investigate the syntypes of *Adamsia involvens* McMurrich, 1893, which had been transferred to *Paracalliactis*, and of its putative synonym *Urticina consors* Verrill, 1882; we redescribe the species as *Paracalliactis consors* (Verrill, 1882). *Adamsia obvolva* and *P. consors* can be distinguished by tentacle number, the inclines on the lower column of specimens of *A. obvolva*, and cnidae distribution and size. The taxonomic changes we propose are summarized in a diagnostic key to actinarian families and genera that live attached to gastropod shells.

We describe *Adamsia obvolva*, a new species of actinarian from the Gulf of Mexico that is symbiotic with the hermit crab *Parapagurus pictus* (Smith, 1883). The pedal disc of the anemone enwraps the gastropod shell in which the hermit crab lives and secretes a thin, chitinous carcinoecium that lies between the pedal disc ectoderm and the shell surface. The carcinoecium also may extend beyond the lip of the underlying shell, enlarging the living chamber of the hermit crab. Association with the hermit crab profoundly affects the anemone's anatomy: the pedal disc diameter is much greater than that of the oral disc, the column is much longer on the side that follows the curve of the gastropod shell than it is on the diametrically opposite side, and some mesenteries are displaced as they grow to follow the curve of the shell.

Specimens of *A. obvolva* we examined from the U.S. National Museum of Natural History (USNM, catalog numbers 50281, 50282, 50287) were misidentified as *Paracalliactis involvens* (McMurrich, 1893); to our knowledge this misidentification has not been recognized in any scientific publication. Members of *A. obvolva* and *P. involvens* both form carcinoecia, and attach to shells inhabited by *Pp. pictus* (see Verrill, 1883, and below). We redescribe *P. involvens* as *P. consors* to reflect the synonymy between *P. involvens* and *Urticina consors* Verrill, 1882 (see Sebens, 1998), and differentiate it from *A. obvolva*.

The original description of *Calliactis* distinguishes it from *Adamsia* based on posture (Verrill, 1869: 481): sea anemones that have a “low growth, spreading to a great extent laterally” were assigned to *Adamsia*, whereas those that are “very changeable in form...

subcylindrical, with a broadly expanded base” were assigned to *Calliactis*. Verrill (1869) further distinguished the two genera based on the shape of the pedal disc: a member of *Adamsia* has a pedal disc with two broad lobes; a member of *Calliactis* has a pedal disc that is roughly circular or ovoid. Carlgren (1928, 1949) used the number of perfect, sterile mesenteries to distinguish *Adamsia* and *Calliactis*: a member of *Adamsia* has two cycles; a member of *Calliactis* has one. Specimens of *A. obvolva* have a lobed pedal disc and a single cycle of perfect, sterile mesenteries. According to Verrill’s (1869) original distinction between *Adamsia* and *Calliactis*, *A. obvolva* belongs in *Adamsia*; Carlgren’s (1928, 1949) criteria would place it in *Calliactis*.

We revise the definitions of *Adamsia* and *Calliactis* to reflect both the original intention of Verrill (1869) and observations and comments made by some previous revisers. For example, Carlgren (1928) noted that members of *Adamsia* are able to secrete a carcinoecium and that those of *Calliactis* lack this ability, but did not include this in his definition. We emphasize the shape of the pedal disc and the secretion of a carcinoecium because the pedal disc shape of members of *Adamsia* and the secretion of a carcinoecium represent a complex of behavioral, anatomical, and biological features that are highly distinctive within Actiniaria.

Mesentery fertility has been used to define genera within Hormathiidae, the family to which these genera belong. Carlgren (1949) distinguished three conditions: first cycle of mesenteries perfect and sterile, first and second cycles of mesenteries perfect and sterile, and first and subsequent perfect cycles fertile. In our revision of *Adamsia*, *Calliactis*, and *Paracalliactis*, we refocus Carlgren’s distinctions to emphasize the shared similarity among members of these genera. In *Adamsia*, *Calliactis*, and *Paracalliactis*, all of the perfect mesenteries are sterile. In our view, the distinction among genera in Hormathiidae is made clearer by recognizing a dichotomy between genera in which the members have sterile perfect mesenteries (regardless of number) and those in which the members have fertile perfect mesenteries (regardless of number).

Although *Adamsia* has been characterized as having two cycles of perfect, sterile mesenteries (e.g., Carlgren, 1928, 1949; Manuel, 1981), and this condition has been reported for its type species, *Adamsia palliata* (Fabricius, 1779) (e.g., Stephenson, 1935), not all reports agree on this feature. Schmidt (1972) reported only a single cycle of perfect sterile mesenteries in specimens of *A. palliata* from the Mediterranean. The value of this feature for defining *Adamsia* is further compromised by the lack of information about this condition in the other two valid species of *Adamsia*. The internal anatomy of *Adamsia fusca* Quoy and Gaimard, 1833, has never been described, and type specimens are unknown. The internal anatomy of *Adamsia sociabilis* Verrill, 1882, is inadequately described because the type material is poorly preserved (Carlgren, 1950).

## METHODS

All specimens of *A. obvolva* we studied were trawled from the Gulf of Mexico, most during the SUCCESS and ALAMINOS expeditions (Table 1). All examined specimens were preserved in ethanol or formalin and stored in 70% ethanol. Specimens are deposited at the following institutions: California Academy of Sciences, San Francisco, California (CAS); Florida Museum of Natural History, Gainesville, Florida (FLMNH); University of Kansas Natural History Museum, Lawrence, Kansas (KUNHM); USNM, Washington, DC; Santa Barbara Museum of Natural History, Santa Barbara, California (SBMNH); Yale University Peabody Museum, New Haven, Connecticut (YPM).

Table 1. Material examined. Locality, depth, and date taken from specimen labels. Type material is indicated in boldface: holotype in *italics*, paratypes in *roman*.

Species	Locality	Depth (m)	Collection date	Museum and catalog number
<i>Adamsia obvolva</i>	N. Gulf of Mexico	538	24 July 1971	<b>CAS 161467; FLMNH 300; KUNHM 001595</b> , KUNHM 001593, 001594, 001596 <b>SBMNH 347281; USNM 1004630</b>
<i>A. obvolva</i>	Gulf of Mexico: 29°21'30"N, 88°21'48.06"W– 29°22'42"N, 88°20'02"W	379–430	24 Feb. 1989	KUNHM 001590; SBMNH 347282
<i>A. obvolva</i>	Gulf of Mexico: 26°35'06"N, 96°16'52"W– 26°26'09"N, 96°13'35"W	505–576	16 June 1989	<b>KUNHM 001591; YPM 28174</b>
<i>A. obvolva</i>	Gulf of Mexico, Louisiana: 27°45'32"N, 19°113'37"W	457–473	11 June 1985	<b>USNM 265293</b> , USNM 1004628, 1004629
<i>A. obvolva</i>	Gulf of Mexico, Louisiana, 128 km off New Orleans	375–400	not given	<b>CAS 052749</b> , CAS 052750
<i>Urticina consors</i>	SSE of Nantucket Island: 39°51'00"N, 69°49'15"W	580	4 Aug. 1881	<b>YPM 9415</b>
<i>Adamsia involvens</i>	Ecuador, Galera Point: 01°03'N, 80°15'W	132	23 March 1883	<b>USNM 17793</b>

Serial sections (8–14  $\mu\text{m}$  thick) of paraffin-embedded specimens were stained with Heidenhain's Azan (Presnell and Schreibman, 1997). Cnidae preparations were made by smearing an approximately 1 mm<sup>2</sup> piece of tissue on a microscope slide; smears from tentacle, column, limbus, actinopharynx, mesenterial filament, and acontium were examined under 1000 $\times$  magnification with differential interference optics. ScanPro measurement software (Jandel Scientific Software) was used to measure the length and width of undischarged cnidae capsules projected onto a Summa Sketch digitizing tablet (Summagraphics). Cnidae nomenclature follows Mariscal (1974). Cnidae presentation follows Dunn et al. (1980).

In the following discussion, "shell" refers to the calcium carbonate gastropod exoskeleton inhabited by the hermit crab host, and "carcinoecium" refers to the chitinous cuticle secreted by the sea anemone. We have rearranged published diagnoses of higher taxa so that they are in parallel, and have clarified terms and definitions that relate to hierarchical levels not included in the discussion. Our additions are indicated in *italics*.

## SYSTEMATIC ACCOUNT

### Order Actiniaria

#### Family Hormathiidae Carlgren, 1932

*Definition*.—*Actiniaria* with *distinct base*. Sphincter mesogleal, strong. Usually six pairs of perfect mesenteries, sometimes more, mesenteries never numerous. *Mesenteries bear acontia*. Mesenteries not divisible into macro- and micro-cnemes. Perfect mesenteries rarely fertile. Nematocysts of the acontia basitrichs only. *Spirocysts usually dimorphic: gracile spirocysts have narrower tubule and smaller capsule than robust spirocysts*. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores. (Modified from Carlgren, 1949)

*Remarks*.—Riemann-Zürneck (1973) reported microbasic *p*-mastigophores from the acontia of a specimen of *Hormathia pectinata* (Hertwig, 1882) [this species was collected during the CHALLENGER expedition and described twice: in German (Hertwig, 1882a) and English (Hertwig, 1882b). The English-language version was translated from the German. Although publications on CHALLENGER materials were to be published in the

English-language CHALLENGER series before being published elsewhere, evidence supports the German-language version as having appeared first (Fautin, 2003)].

### Genus *Calliactis* Verrill, 1869

*Type species.*—*Actinia decorata* Dana, 1846

*Diagnosis.*—Hormathiidae with *circular or oval pedal disc. Pedal disc equal to or only slightly larger in diameter than oral disc, does not secrete carcinoecium.* Members of species belonging to this genus live attached to rocks, gastropod shells, worm tubes, or other substrates. Column smooth, with cinclides in proximal part, not or only slightly differentiated into scapus and scapulus, the former of which may have a weak cuticle. *Column diameter typically less than column height.* Column nematocysts basitrichs only. Tentacles in several cycles, as numerous as mesenteries proximally. Six pairs of perfect, sterile mesenteries, two pairs of directives, each attached to a siphonoglyph. Retractor and parietobasilar muscles weak. (Modified from Verrill, 1869; Carlgren, 1949; Hand, 1975a)

### Genus *Adamsia* Forbes, 1840

*Type species.*—*Actinia palliata* Fabricius, 1779.

*Diagnosis.*—Hormathiidae with *pedal disc divisible into two lobes. Pedal disc of greater diameter than oral disc, secretes carcinoecium.* Species belonging to this genus live attached to gastropod shells inhabited by hermit crabs. Column smooth, with cinclides at mid-column, not or only slightly differentiated into scapus, scapulus, and capitulum. *Column diameter greater than column height.* Column nematocysts basitrichs only. Tentacles in several cycles, more numerous than mesenteries proximally. *Six or twelve* pairs of perfect, sterile mesenteries, two pairs of directives, each attached to a siphonoglyph. *Retractor and parietobasilar muscles weak.* (Modified from Carlgren, 1949)

*Taxonomic Remarks.*—The first description of the type species of this genus was that of Bohadsch (1761), who described it as *Medusa palliata*. As Manuel (1981) pointed out, the International Code of Zoological Nomenclature (ICZN, 1999) ruled that all names erected by Bohadsch (1761) are invalid for the purpose of nomenclature (Hemming, 1944). According to Manuel (1981), the first available name for the species is *Actinia carciniopados* Otto, 1823, because *Actinia maculata*, a name given to it by Adams (1800), is preoccupied. However, a re-description of *M. palliata* by Fabricius (1779) that predates both Adams (1800) and Otto (1823) meets all requirements of the ICZN. The type species of *Adamsia* is thus *M. palliata* Fabricius, 1779; the valid name of the species is *Adamsia palliata* (Fabricius, 1779).

### *Adamsia obvolva* new species

(Figs. 1–4)

*Column.*—All examined specimens preserved, contracted, pale pink to cream (Fig. 1). Column with short capitulum (Fig. 1A,C). Large cinclides at mid-column (Fig. 1B). In examined specimens, contracted height of longest side 27–42 mm, width 22–38 mm.

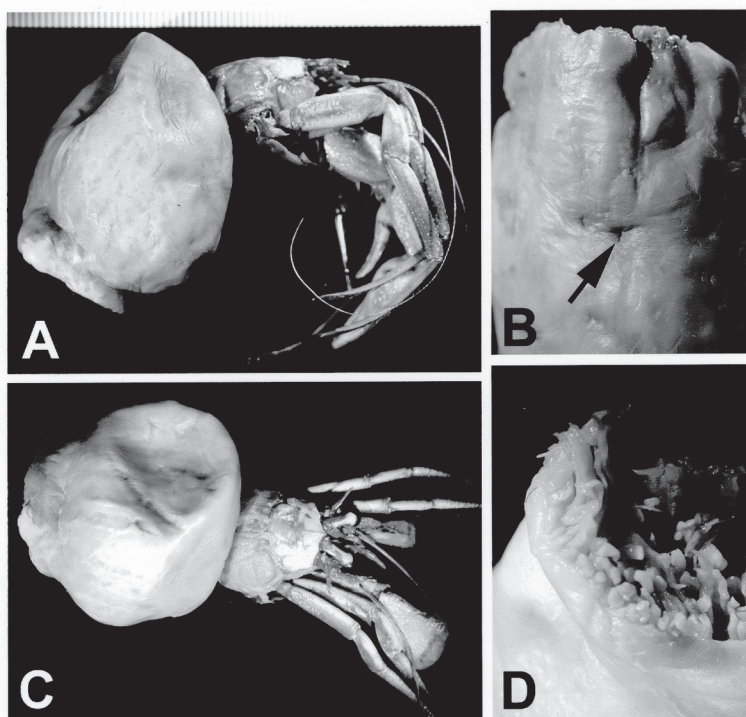


Figure 1. External anatomy of *Adamsia obvolva* n. sp. Scale in mm. A) Lateral view of specimen attached to hermit crab; oral disc at left. B) Detail of column, cinclide indicated with arrow. Oral disc at top. C) Top view of specimen shown in Fig. 1A. D) Detail of distal end, showing tentacles, margin, and sunken oral disc.

**Oral Disc and Tentacles.**—In preserved specimens, oral disc directed away from shell aperture and anterior of hermit crab (Fig. 1A,C). In retracted animals, oral disc sunken (Fig. 1D). Tentacles short, marginal (Fig. 1D), approximately equal in thickness entire length, with ectodermal longitudinal muscles. Ectoderm of tentacles thick, with microscopic transverse ribs (Fig. 2A). Tentacles to 250; arrangement and number of cycles unclear. Inner tentacles 4–7 mm long in contracted specimens; outer tentacles one half or one third as long as inner.

**Pedal Disc and Carcinoecium.**—Pedal disc wrapped around gastropod shell inhabited by hermit crab (Fig. 1A), highly glandular, secretes bronze-colored, thin, papery carcinoecium (Fig. 2B,3) which may extend beyond shell aperture. Carcinoecium finely wrinkled along spire, with umbilicus (Fig. 3B); ornamentation (Fig. 3C) reflects that of underlying gastropod shell. In all specimens examined, column longitudinal axis parallel to columella of shell. Pedal disc diameter of specimens examined 23–41 mm.

**Mesenteries and Internal Anatomy.**—Marginal sphincter (Fig. 2C) lies against ectodermal side of body wall, transversely striated, with many small, densely packed alveoli, one half to three quarters width of mesoglea in distal column, tapering proximally on both ectodermal and endodermal sides. Mesenteries in four or five cycles; mesenteries of highest cycle only at distal end, regularly arranged but minute, imperfect. Larger mesenteries with oral and marginal stomata. Mesenteries of first cycle, including directives, perfect and sterile; mesenteries of second and third cycle imperfect, fertile, with ciliated filaments. Gonochoric. Acontia long, thin, tightly coiled, arise mid-way along



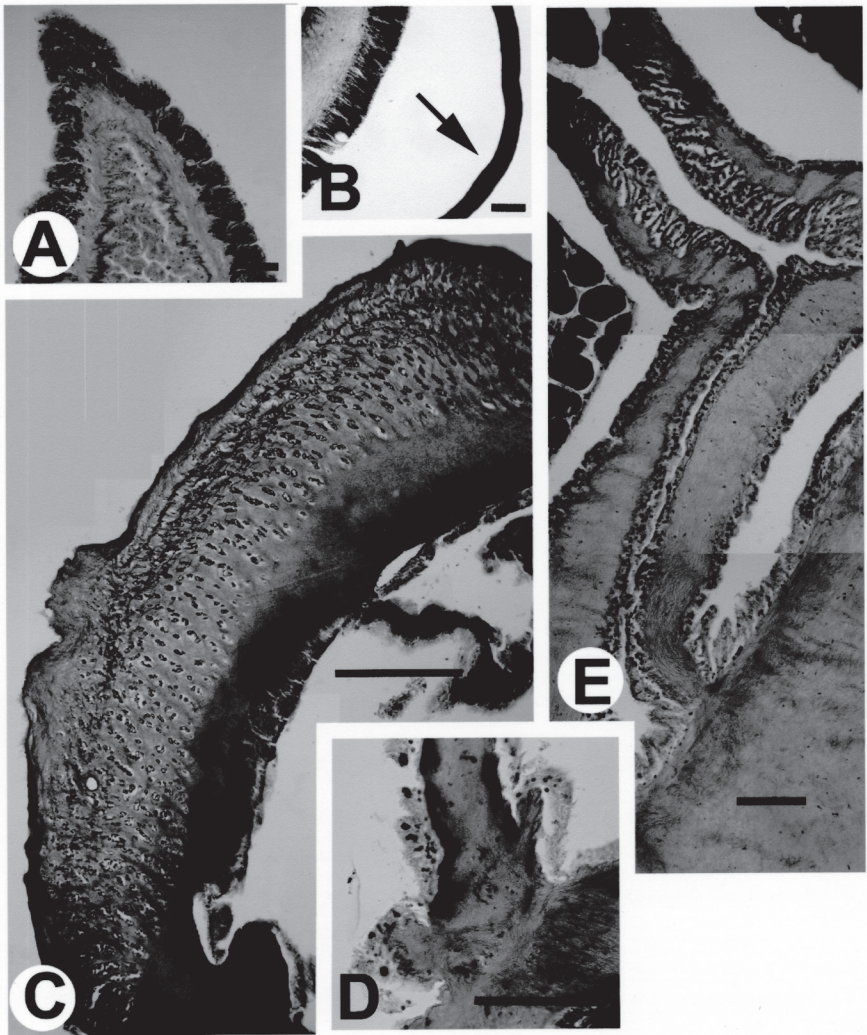


Figure 2. Internal anatomy of *Adamsia obvolva* n. sp. A) Longitudinal section through an outer tentacle. Transverse ridges of ectoderm not noticeable macroscopically. Scale = 50  $\mu$ m. B) Transverse section through pedal disc, showing ectoderm and carcinocoeum (arrow), which has separated from ectoderm. Scale = 50  $\mu$ m. C) Longitudinal section through marginal sphincter; distal end at top. Scale = 0.5 mm. D) Longitudinal section through pedal disc, showing basilar muscles. Scale = 30  $\mu$ m. E) Transverse section through column and mesenteries in region proximal to actinopharynx. Scale = 100  $\mu$ m.

mesentery. Basilar muscles weak (Fig. 2D). Retractor and parietobasilar muscles diffuse, weak (Fig. 2E).

*Cnidom.*—Spirocysts, basitrichs, microbasic *p*-mastigophores (Fig. 4). See Table 2 for size and distribution.

*Symbiont.*—*Parapagurus pictus*.

*Type Locality and Recorded Distribution.*—Gulf of Mexico, 375–550 m.

*Etymology.*—Nominative singular of the Latin *obvolvo*, meaning to wrap or envelop. This refers to the posture of the species, and relates to the colloquial appellation “wrap-

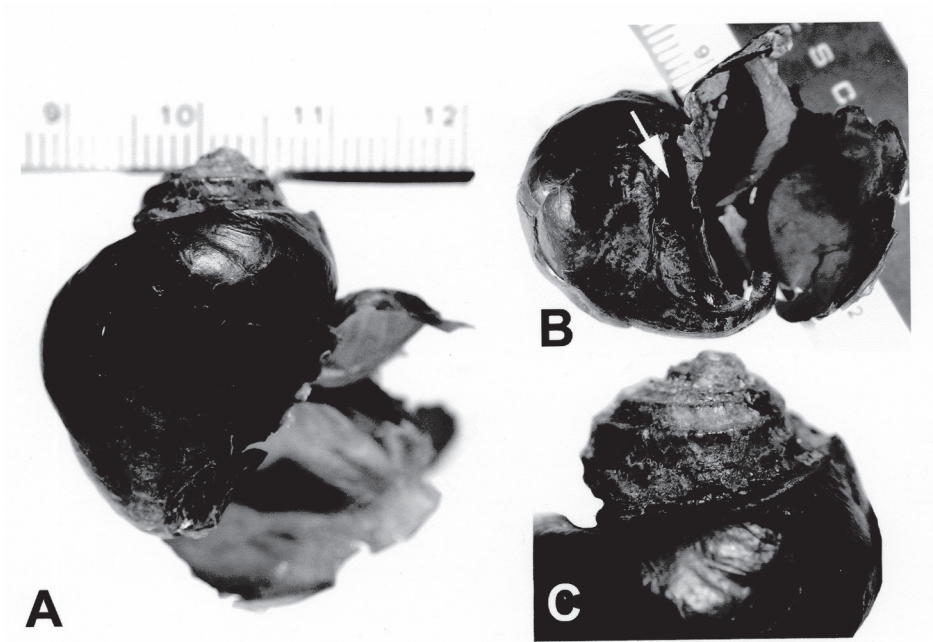


Figure 3. Carcinoecium of *Adamsia obvolva* n. sp. Scale in mm. A) Aperture view. B) View from below; arrow indicates umbilicus. C) Apex of carcinoecium, showing spire and ornamentation impressed on carcinoecium from underlying shell.

Table 2. Size and distribution of cnidae of *Adamsia obvolva*. Letters refer to Fig. 4; "N" is the proportion of examined specimens that had a particular type of cnida, "n" is the number of cnidae measured. Size is presented as range of lengths by widths, in  $\mu\text{m}$ ; numbers in parentheses are single measurements that fell outside the range. Column cnidae were sampled separately from the upper column, mid-column, and limbus, but were indistinguishable, so measurements were pooled.

Tissue	Cnida type	N	n	Size
tentacle	robust spirocyst (A)	8/8	79	18.1–48.1 $\times$ 3.2–10.3
	gracile spirocyst (B)	8/8	106	15.8–30.3 $\times$ 2.2–4.4
	microbasic <i>b</i> -mastigophore (C)	8/8	204	14.9–29.7 (38.0) $\times$ 2.0–5.1 (5.7)
	small basitrich (D)	8/8	69	7.2–14.5 $\times$ 1.2–3.3
column	basitrich (E)	5/5	148	15.8–34.3 $\times$ 2.3–4.2
	small basitrich (D)	5/5	97	6.5–14.1 $\times$ 0.9–3.1
	microbasic <i>p</i> -mastigophore (G)	3/5	10	22.5–30.2 $\times$ 1.7–5.4
actinopharynx	large basitrich (F)	7/7	66	(13.6) 15.4–38.8 $\times$ 2.0–4.5
	microbasic <i>p</i> -mastigophore (G)	7/7	54	20.1–40.0 $\times$ 3.0–6.7
filament	basitrich (E)	6/6	60	16.3–30.1 $\times$ 2.3–5.0
	small basitrich (D)	6/6	47	8.25–16.5 $\times$ 1.1–3.4
	microbasic <i>p</i> -mastigophore (G)	6/6	130	17.9–28.3 $\times$ 3.2–5.1
acontium	large basitrich (F)	8/8	173	22.3–51.3 $\times$ 3.2–5.7
	small basitrich (D)	8/8	74	10.3–21.2 $\times$ 1.4–3.5

per anemone” used by M. Wicksten, a hermit-crab taxonomist who provided us with specimens.

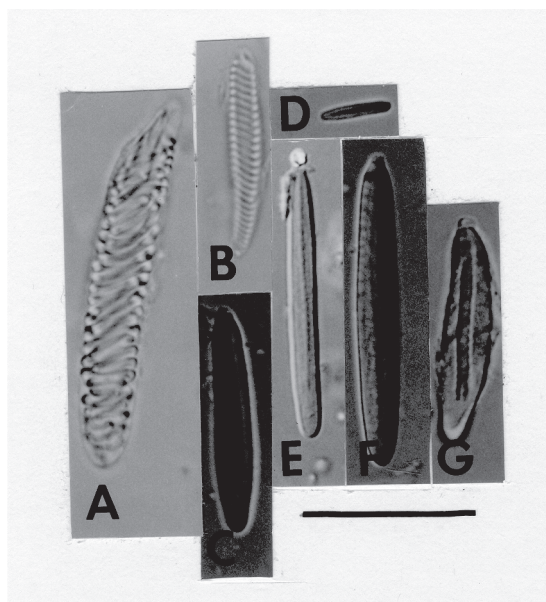


Figure 4. Cnidae of *Adamsia obvolva* n. sp. Scale = 15  $\mu$ m. A) Robust spirocyst. B) Gracile spirocyst. C) Microbasic *b*-mastigophore. D) Small basitrich. E) Basitrich. F) Large basitrich. G) Microbasic *p*-mastigophore.

### Genus *Paracalliactis* Carlgren, 1928

*Type species.*—*Paracalliactis valdiviae* Carlgren, 1928

*Diagnosis.*—*Hormathiidae* with pedal disc in two lobes. Pedal disc of greater diameter than oral disc, secretes carcinoecium. Species belonging to this genus live attached to gastropod shells inhabited by hermit crabs. Column smooth or with distal tubercles, without cinclides, divisible into scapus and scapulus; may have a thin, easily deciduous cuticle. Column diameter greater than column height. Column nematocysts microbasic *p*-mastigophores and basitrichs. Tentacles in several cycles, about the same number as mesenteries proximally. Six pairs of perfect and sterile mesenteries, two pairs of directives, each attached to a siphonoglyph. Retractor and parietobasilar muscles weak. (Modified from Carlgren, 1928, 1949; Hand, 1975a)

### *Paracalliactis consors* (Verrill, 1882) new combination

(Fig. 5)

*Urticina consors* Verrill, 1882, p. 225; Verrill, 1883, p. 49

*Actinauge consors* Verrill, 1885, p. 534

*Adamsia involvens* McMurrich, 1893, p. 182

*Paracalliactis involvens* Carlgren, 1947, p. 15; Carlgren, 1949, p. 95; Sebens, 1998, p. 53

*Column.*—All examined specimens preserved, contracted, conical, translucent yellowish-cream (Fig. 5). Column divisible into scapulus and scapus: border between scapus and scapulus may bear variable number of imperforate tubercles (Fig. 5C). Scapus



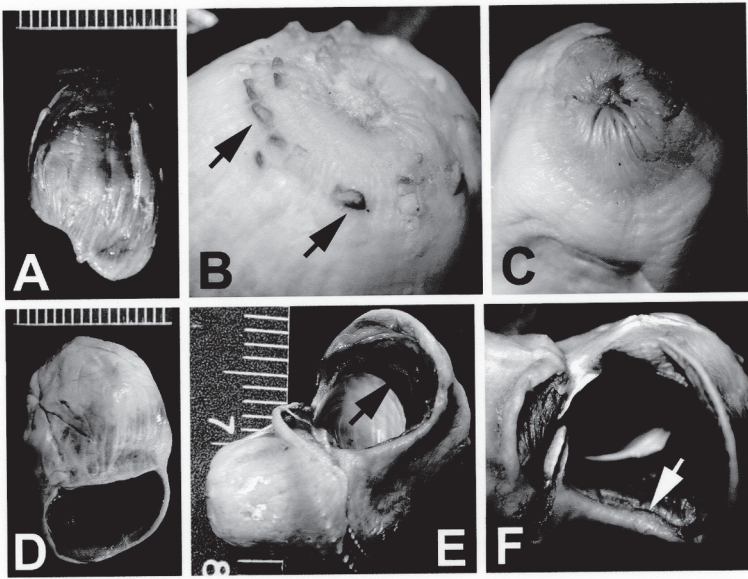


Figure 5. External anatomy of *Paracalliactis consors* n. comb. Scale in mm. A) *Adamsia involvens* syntype, lateral view, with oral disc at top. Column longer on right side than on left. B) Detail of distal column of *Urticina consors* syntype. Two rows of tubercles (arrows) ring scapulus. C) Detail of distal column of *Adamsia involvens* syntype. This specimen lacks tubercles on the scapulus. D) *Adamsia involvens* syntype, lateral view. Specimen is rotated 180° along oral-aboral axis relative to animal in Fig. 5A. E) Anterior view of two *U. consors* syntypes attached to a single gastropod shell. Carcinoecium (arrow) extends beyond aperture of shell. F) Posterior view of Fig. 5E, showing single shell aperture. Note thickened ectoderm at junction of limbus and carcinoecium (arrow).

smooth, without cuticle, translucent, crenulated, with longitudinal plications (Fig. 5B). Scapulus also without cuticle, thinner and more translucent than scapus (Fig. 5A,D). In examined specimens, height of longest side 18–30 mm, diameter 16–23 mm.

**Oral Disc and Tentacles.**—In preserved specimens examined, oral disc directed away from shell aperture and anterior of hermit crab. In retracted specimens, oral disc sunken. Tentacles marginal, short, of equal thickness along length, 60–96 in number, in three or four cycles.

**Pedal Disc and Carcinoecium.**—Pedal disc wrapped around gastropod shell inhabited by hermit crab, highly glandular, secretes thin, chitinous carcinoecium (Fig. 5E,F) which may extend beyond shell aperture. Limbus thickened, rolled at junction with carcinoecium (Fig. 5F). Column perpendicular to columella of shell; apex of shell may distort column wall.

**Mesenteries and Internal Anatomy.**—Marginal sphincter lies against ectodermal side of body wall, with weak transverse striations, one third to one half width of mesoglea of distal column, tapering proximally on both endodermal and ectodermal sides (pers. obs; fig. 85, McMurrich, 1893). Mesenteries in three or four cycles; approximately same number of mesenteries proximally and distally. Larger mesenteries with oral and marginal stomata. Mesenteries of first cycle, including directives, perfect and sterile; mesenteries of second and third cycles imperfect, fertile, with ciliated filaments. Retractor and parietobasilar muscles diffuse, weak.

*Cnidom.*—Spirocysts, basitrichs, microbasic *p*-mastigophores. See Table 3 for size and distribution.

*Symbiont.*—No hermit crab was preserved with syntypes of either *U. consors* or *P. involvens*. Verrill (1883) and Balss (1924) reported that *U. consors* associates with *Pp. pictus*.

*Taxonomic Remarks.*—Carlgren (1947) transferred *A. involvens* to *Paracalliactis*; we agree that this is the appropriate genus for this species. We agree with Sebens (1998) that *U. consors* Verrill, 1882, and *A. involvens* McMurrich, 1893, are synonyms. However, because *U. consors* is the older name, and because neither name has been used recently in publication except in Sebens' (1998) faunal guide, the species should be called *P. consors* (Verrill, 1882) not *P. involvens* as given by Sebens (1998) (Art. 23.9.1, ICZN 1999).

#### DIFFERENTIAL DIAGNOSIS AND DISCUSSION

**DIFFERENTIAL DIAGNOSIS.**—*Adamsia obvolva* is the only species of this genus reported from the Gulf of Mexico. Two species of *Calliactis*, *C. variegata* (Verrill, 1869), and *C. tricolor* (Le Sueur, 1817), have geographic ranges that overlap with that of *A. obvolva*. However, members of neither species make carcinoecia, and the bathymetric ranges of these species differ from that of *A. obvolva*: *C. tricolor* is intertidal and *C. variegata* is from the shallow subtidal (3.7–11 m), whereas *A. obvolva* is known from approximately 300–575 m.

The geographic range of *P. consors* includes the Gulf of Mexico (Table 1). Members of *P. consors* and *A. obvolva* live at similar depths, are commensal with *Pp. pictus*, and secrete carcinoecia. Accurate identification is further complicated by the fact that members of these two species are of similar size and have similar mesentery arrangement and tentacle and muscle morphology (compare Figs. 1, 2C,E, 3, and 5 with figs. 82–85; McMurrich, 1893). Two noteworthy external features distinguish *P. consors* and *A. obvolva*. The column of *P. consors* lacks cinclides whereas the column of *A. obvolva* bears cinclides. *Paracalliactis consors* has approximately half as many tentacles as *A. obvolva*. Several cnidae features further distinguish *A. obvolva* and *P. consors*: the column ectoderm of a specimen of *A. obvolva* lacks microbasic *p*-mastigophores whereas the column of a specimen of *P. consors* contains microbasic *p*-mastigophores, and the size of the tentacle basitrichs, filament microbasic *p*-mastigophores, and acontia basitrichs differ in the two species. However, the size ranges of other cnidae largely overlap (compare Tables 2 and 3). Syntypes of *P. consors* lack small basitrichs in the tentacles, but this difference may be an artifact of tissue quality and sample size rather than a real difference between *A. obvolva* and *P. consors*.

**SYNONYMY OF *P. INVOLVENS* AND *U. CONSORS*.**—Our account of the anatomy of *P. consors* differs from previous accounts in a few respects. McMurrich (1893) indicated that live *P. involvens* have a tentaculate margin; all preserved syntypes have a deep channel separating the column from the tentacles. Based on his study of live and preserved *Paracalliactis* specimens, Hand (1975a) suggested that this channel, which Carlgren (1928, 1949) equated with a fosse, was a preservational artifact. Our observations and McMurrich's (1893) report support Hand's (1975a) interpretation.

The tentacles of *P. involvens* are arranged in three cycles (McMurrich, 1893); Verrill (1882, 1883) estimated that *U. consors* has four cycles of tentacles. We found that the number of tentacles in syntypes of both nominal species is larger than 60, but does not

Table 3. Size and distribution of cnidae of *Paracalliactis consors*: syntypes of *Urticina* consors and *Paracalliactis involvens* are shown separately; n is the number of cnidae measured, dimensions are given in  $\mu\text{m}$ . Cnidae measurements given in Carlgren (1947) for *P. involvens* have been included for comparison.

Tissue	Cnida	n	<i>U. consors</i>	n	<i>P. involvens</i>	<i>P. involvens</i> from Carlgren
tentacle	spirocyst	17	19.7–38.5 $\times$ 2.4–5.0	34	16.7–50.7 $\times$ 2.6–7.9	
	basitrich	20	19.2–26.9 $\times$ 2.0–3.1	15	21.5–26.5 $\times$ 2.8–3.9	19.7–22.6 $\times$ 2.8–3.5
	wide basitrich	62	22.6–26.8 $\times$ 3.6–4.4			up to 52 $\times$ 8.5
filament	basitrich	15	12.4–16.2 $\times$ 1.4–2.2	29	11.6–18.0 $\times$ 1.5–2.8	12.7–15.5 $\times$ ~2
	basitrich	17	27.8–37.2 $\times$ 2.6–3.9	20	24.2–32.3 $\times$ 3.0–4.5	
	microbasal <i>p</i> -mastigophore	10	25.3–33.8 $\times$ 2.9–3.8	18	20.3–31.7 $\times$ 3.5–5.0	19.7–23.3 $\times$ 3.5–4.2
acontium	basitrich	16	28.6–36.3 $\times$ 2.8–3.4			22.6–28.2 $\times$ 2.8–3.5
	basitrich	51	4.0–17.8 $\times$ 1.1–1.5			

exceed 96. Assuming that the tentacles of this species are arranged hexamerously as in other hormathiids, the tentacles are arranged in 3–4 cycles.

The condition of syntypes of *U. consors* and *P. involvens* preclude direct observation of certain aspects of the anemone's anatomy. Some specimens lack a gastropod shell, but ornamentation of the carcinoecium indicates its initial presence. Although no hermit crabs are preserved with syntypes of either *U. consors* or *P. involvens*, both Verrill (1883) and Balss (1924) reported that *U. consors* is symbiotic with *Pp. pictus*. Although we were unable to find acontia in the *A. involvens* syntypes, McMurrich (1893) observed acontia in living specimens, and Carlgren (1947) measured cnidae from the acontia of specimens from the syntype lot.

Some syntypes of *U. consors* have a crown of tubercles on the distal column; none of the *A. involvens* syntype specimens bear tubercles. Because these tubercles are on only some *U. consors* specimens, we regard them as individual or preservational variation. Although cnidae size ranges are the same in *U. consors* and *P. involvens*, the spirocysts of *U. consors* are smaller than those of *P. involvens* (Table 3). Two *U. consors* syntypes share a single gastropod shell (Fig. 5E,F). Shell sharing is not seen in any of the specimens of *P. involvens* we examined, and is rare among carcinoecium-forming species.

The most significant difference between *P. involvens* and *U. consors* is their reported geographic range: *U. consors* was described from the western North Atlantic Ocean and *P. involvens* was described from the eastern Pacific Ocean (Table 1). However, we detect no consistent anatomical difference between the syntypes of *P. involvens* and *U. consors*, and the range of the hermit crab that hosts both *P. involvens* and *U. consors* spans this distance.

**TAXONOMY OF ACTINIARIANS LIVING ATTACHED TO SHELLS INHABITED BY HERMIT CRABS.**—Using the presence or absence of cinclides or carcinoecia rather than the number of sterile mesenteries to distinguish between hormathiid species that live attached to gastropod shells inhabited by hermit crabs facilitates identification, especially of infertile specimens. We interpret a second cycle of perfect, sterile mesenteries as a unique feature of *A. palliata*, rather than characteristic of the genus *Adamsia*. Although the changes we have made to the generic definitions clarify distinctions among *Adamsia*, *Calliactis*, and *Paracalliactis*, the characters we have used to distinguish these genera may not be of phylogenetic or taxonomic significance in the broader context of all Hormathiidae. The contradictions and inconsistencies we discovered in the diagnoses of *Adamsia* and *Calliactis* indicate that a thorough revision of all members of Hormathiidae is needed to address the generality, variability, and relative importance of systematic characters.

Sea anemones that live attached to gastropod shells inhabited by hermit crabs belong to at least six genera in four families: Actiniidae (*Stylobates* Dall, 1903), Hormathiidae (*Adamsia*, *Calliactis*, *Paracalliactis*), Sagartiidae (*Carcinactis* Uchida, 1960; *Verrillactis* England, 1971; gen., sp. indet., Ross and Wada, 1975), and Sagartiomorphidae (gen., sp. indet., Ross and Wada, 1975) (Table 4). Members of *Adamsia*, *Paracalliactis*, and *Stylobates* secrete carcinoecia. A member of *Stylobates* can be distinguished from members of the other carcinoecium-secreting genera by its endodermal sphincter muscle and lack of acontia (Dunn et al., 1981); both of these features are typically visible only in dissected specimens. Members of Hormathiidae, Sagartiidae, and Sagartiomorphidae are distinguished by the type of nematocysts in the acontia: hormathiids have only basitrichs, sagartiids have basitrichs and microbasic amastigophores, and sagartiomorphids have only microbasic amastigophores (Carlgren, 1949).

Table 4. A key to actiniarian families and genera that include species that live attached to gastropod shells inhabited by hermit crabs.

1A. With acontia, sphincter mesogleal	2
1B. Without acontia, sphincter endodermal	<i>Stylobates</i>
2A. Acontia contain a single type of nematocyst	3
2B. Acontia contain two (or more) types of nematocysts	Sagartiidae, 6
3A. Acontia nematocysts basitrichs	Hormathiidae, 4
3B. Acontia nematocysts amastigophores	Sagartiomorphidae
4A. Column with cinclides	5
4B. Column without cinclides	<i>Paracalliactis</i>
5A. Pedal disc lobed, with carcinoecium	<i>Adamsia</i>
5B. Pedal disc oval or circular, without carcinoecium	<i>Calliactis</i>
6A. Acontia with two types of amastigophores and one type of basitrich, mesenteries divisible into macrocnemes and microcnemes	<i>Carcinactis</i>
6B. Acontia with one type of amastigophore and two types of basitrichs, mesenteries not divisible into macrocnemes and microcnemes	<i>Verrillactis</i>

BIOLOGY OF ACTINIARIANS LIVING ATTACHED TO SHELLS INHABITED BY HERMIT CRABS.—When the sea anemone is attached to a shell inhabited by a hermit crab at least three possible types of benefits occur: phoretic, defensive, and trophic (see Dunn et al., 1981, for a review). An otherwise sessile anemone is transported by the crab, increasing its dispersal potential and access to food or suitable habitat (Ross, 1974; Dunn et al., 1981). Some hermit crabs will move away from animals attempting to prey on their attached sea anemones (Brooks and Gwaltney, 1993), and some species of hermit crabs fight or ingest predators of sea anemones (Brooks and Gwaltney, 1993). Prey items (or pieces thereof) captured by the hermit crab may be eaten by the sea anemone (Ross, 1984). The hermit crab receives protection from the sea anemone, the nematocysts of which can deter octopods and other hermit crab predators (Ross, 1971; McLean and Mariscal, 1973; Hand, 1975b).

The degree of association and the particulars of the interaction vary between species of hermit crab and of sea anemone. Carcinoecium-forming sea anemones are probably obligate symbionts (Dunn et al., 1981). In all sea anemone species studied so far, the interaction is not partner-specific (Balss, 1924; Ates, 1995). The hermit crabs are more partner-specific than the sea anemones; some hermit crabs are able to discriminate between species of potential symbionts (Cutress and Ross, 1969; Hand, 1975b; Ross and Wada, 1975). *Adamsia obvolva* is sympatric with a zoanthidean (Cnidaria: Anthozoa: Zoanthidea) that also attaches to shells inhabited by hermit crabs; the zoanthidean associates with both *Parapagurus pilosimanus* Smith, 1879, and *Pp. pictus*. To our knowledge, *A. obvolva* is never found with *Pp. pilosimanus*.

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